

Additions to Knowledge of the Early Pleistocene Wallaby, *Baringa nelsonensis* Flannery and Hann 1984 (Marsupialia: Macropodinae)

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Following the recovery of more specimens of the extinct wallaby, *Baringa nelsonensis*, from early Pleistocene deposits at Nelson Bay, near Portland, Victoria, dental elements that were previously unknown, or only tentatively associated with *Baringa* at the time of its establishment, are described here. Specimens from the early Pliocene Curramulka Local Fauna, Yorke Peninsula, South Australia, previously allied with *Baringa*, are re-examined, and it is concluded that they do not belong to this genus. *Baringa* is an intermediate browser-grazer, but the relatively enlarged I¹ and characteristic vertical wear facet on I₁ suggest an unusual feeding specialisation.

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INTRODUCTION

Baringa nelsonensis is a small to medium-sized macropodine first described by Flannery and Hann (1984) from the early Pleistocene Nelson Bay Local Fauna (LF), Portland, Victoria (Hann 1983). It is the most abundant species in the fauna, accounting for approximately 30% of all specimens. Further collection and study of *Baringa* material from Nelson Bay was reported by Herrmann (2000), who described much of the new material, including teeth previously unknown at the time of the original description of *Baringa*. Collecting is still being carried out at Nelson Bay, and current research on the fauna by one of us (K. P.) has produced more dental specimens referable to *B. nelsonensis*.

Upper incisors and premolars are often highly diagnostic of genera within the Macropodidae. This paper describes elements of the incisor and premolar dentition previously unknown for the genus. In addition, following the discovery of an upper deciduous premolar (dP²) in association with undoubted *Baringa* upper molars, the single dP² specimen (NMV P173573) referred to *Baringa* by Flannery and Hann (1984) is no longer considered correctly assigned. Other features of the dentition are also discussed based on the more complete material

now available.

In addition to the Nelson Bay specimens, specimens tentatively aligned with *Baringa* (cf. *Baringa* sp., cf. *Baringa nelsonensis*) have been reported from the Curramulka Local Fauna (Pledge 1992). The affinities of these specimens have been re-examined in the light of the new, more complete topotypic material.

All *Baringa* specimens described here are registered in the palaeontology collection of Museum Victoria (NMV P). A full list of specimens examined is given in the Appendix. The Curramulka Local Fauna specimens are registered in the palaeontology collection of the South Australian Museum (SAM P), a list of which is given in Pledge (1992).

Classification within the Macropodidae follows Kear and Cooke (2001) and dental terminology follows Luckett (1993). All measurements are in millimetres.

SYSTEMATICS

Order: Diprotodontia Owen, 1866
Family: Macropodidae Gray, 1821
Subfamily: Macropodinae Gray, 1821
Tribe Macropodini Flannery, 1989
Baringa nelsonensis Flannery and Hann, 1984

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Description

Deciduous Premolars:

Eight dP_2 s are known, three of which are certainly associated with *Baringa nelsonensis* molars (Fig 1j). They consist of a simple blade with a prominent anterior cuspid, posterior cuspid, and a single intermediate cuspile and associated ridgelet, all of which are approximately sub-equal in height. The anterior cuspid is occasionally slightly lower and is separated from the intermediate cuspile by a deep groove. The main blade terminates anteriorly in a small, low, rounded cuspile. A small, lower posterolingual cuspid is also present, separated from the posterior cuspid by a shallow groove. A second smaller cuspile is present posterior to the posterolingual cuspid in NMV P200410 (Figs 1a-c;

Table 1).

Nine complete dP^2 s are known, five of which are certainly associated with *B. nelsonensis* molars (Fig 1k). They are all morphologically similar, consisting of a main blade, a posterolingual cusp and a very poorly-developed, lingual cingulum. The blade consists of a well-defined anterior and posterior cusp with a single intermediate cuspile and ridgelet, which often appears to be merged with the posterior cusp. The posterior cusp is higher than the anterior cusp. The anterior cusp is separated from the intermediate cuspile by a groove. The weak lingual cingulum comprises a low, narrow bulge extending from the posterolingual cusp, and terminating at a small anterolingual tubercle. The posterolingual cusp is lower than the main crest and is separated from the lingual cingulum and posterior

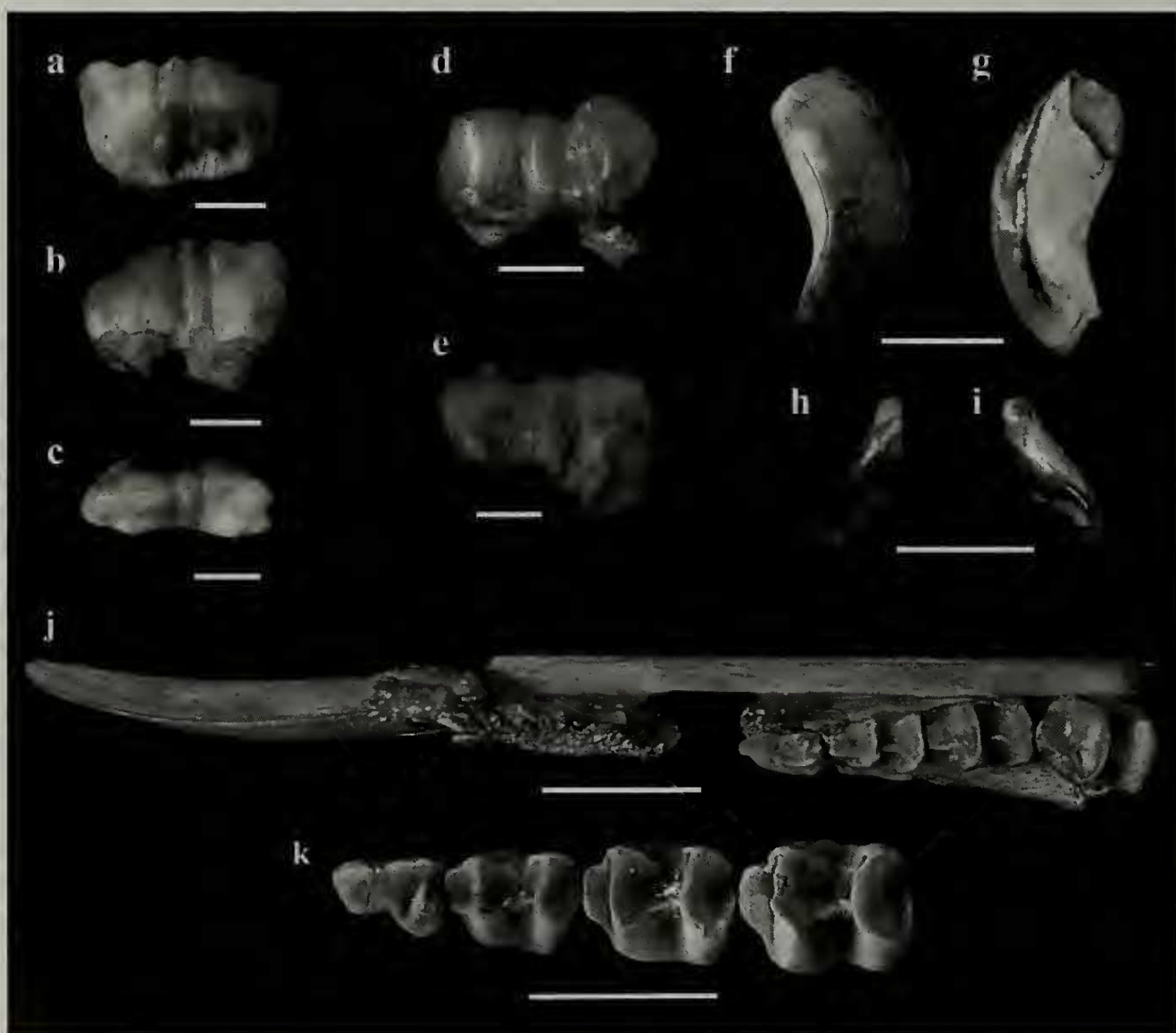


Figure 1. *Baringa nelsonensis*. (a) NMV P200449 right dP_2 labial view, (b) lingual view, (c) occlusal view, (d) NMV P200482 left dP^2 labial view, (e) occlusal view. Scale bar = 2 mm, (f) NMV P216028 right I^1 buccal view, (g) lingual view (h) NMV P200702 left I^2 labial view, (i) lingual view, (j) NMV P200410 left dP_2 , dP_3 , M_{1-2} in dentary fragment with associated I_1 occlusal view, (k) NMV P201155 left associated dP^2 , dP^3 , M^{1-2} occlusal view. Scale bar = 10 mm.

Table 1. Dimensions (mm) of *Baringa nelsonensis* deciduous premolars. L = length, AW = anterior width, PW = posterior width.

Specimen	dP ₁			dP ₂		
	L	AW	PW	L	AW	PW
NMV P200410	5.4	2.5	2.7			
NMV P200449	5.7	2.4	2.6			
NMV P200450	5.9	2.3	-			
NMV P200690	-	-	2.5			
NMV P201155	5.5	2.0	2.4			
NMV P215777	5.5	2.6	2.8			
NMV P215789	5.7	2.5	2.5			
NMV P215790	5.3	2.4	2.8			
NMV P200444				5.6	3.0	3.9
NMV P200482				5.8	3.1	4.1
NMV P201155				6.3	3.0	4.1
NMV P215774				5.7	2.9	4.0
NMV P215777 (R)				6.1	3.2	4.4
NMV P215777 (L)				6.0	3.3	4.4
NMV P215966				6.5	3.3	4.0
NMV P216888				5.8	3.2	-

cuspid by a deep groove. A weakly developed medial posterior fossette is present (Figs 1d-e; Table 1).

Upper incisors:

Sixteen partial and complete I¹s are known. They are large relative to the size of I² and the molar teeth, a condition similar to that seen in *Protemnodon*. They are arc-shaped, possessing a convex labial surface, which is twisted slightly medially to bring the anterior-most tips into contact. They are widest near the root (7.2 mm), tapering slightly towards the tip (6.3 mm unworn). A moderately thick enamel covers the labial surface, extending over the sharply curved anterior edge onto the anterolingual surface to form a wide band. The lingual surface is only thinly enamelled close to the tip, which is removed by wear. The labial surface is occasionally ornamented by fine grooves and ridgelets, which follow the curvature of the tooth. They are similar morphologically to the I¹ of *Protemnodon*, but are readily distinguished, being smaller, less robust, and are narrower buccolingually, therefore producing a much smaller occlusal wear facet (2.7 mm average width) (Figs 1f-g; Table 2).

Unfortunately none of the I¹s have been found in

association with *B. nelsonensis* cheek teeth. They are here assigned to *B. nelsonensis* as they are relatively abundant in the assemblage, are too small to be referable to either *Protemnodon brehus*, *P. roechus* or *P. sp. nov.* present in the fauna, and too large to be referred to any other genus of macropodid identified so far in the Nelson Bay Local Fauna.

At the time of its description, only one moderately worn I² (NMV P173591 originally identified as I³) was known for *B. nelsonensis*, and was not associated with any other specimens (Flannery and Hann 1984). Eight unworn complete and partial I²s are now known, but still none are associated with other *B. nelsonensis* material. However, they are relatively abundant in the assemblage, and are not referable to any other genus in the Nelson Bay Local Fauna, so their assignment to *B. nelsonensis* is still followed here. Many of the specimens lack a lingual surface due to damage, but they are all similar in morphology to NMV P173591, being narrow anteroposteriorly, and in possessing a short labial groove very close to the posterior edge, which continues onto the occlusal surface. The occlusal edge is notched approximately halfway along its length. The prominent cuspid at

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Table 2. Occlusal length (mm) of *Baringa nelsonensis* upper incisors. OL = occlusal length, e = estimated.

	NMV P173648	NMV P216022	NMV P216023	NMV P216024	NMV P216027	NMV P216027	NMV P216028	NMV P216032	NMV P216035	NMV P216145a	NMV P173591	NMV P200702	NMV P215806	NMV P215810	NMV P215871	NMV P215992b	NMV P216202	NMV P216224	
I1																			
OL	6.2	6.1	6.4	7.0	6.9	7.5	6.1	7.4	7.6	7.2									
I2																			
OL											4.3	5.0	5.1	4.8e	5.3	5.1	5.4	5.1	

the posterior end of the occlusal crest present in NMV P173591 is variably developed in the present sample (Figs 1h-i; Table 2).

Remarks

The dP²s described above differ from NMV P173573, the isolated dP² originally referred to *Baringa* by Flannery and Hann (1984) in the following details: they are shorter and broader; possess only one intermediate cuspule instead of two; lack a sharp lingual ridge on the anterior cusp; the posterior cusp is the highest, and is separated from the posterolingual cusp by a groove. NMV P173573 is very similar in both size and form to the P³ of *Thylogale billardierii*. This genus has since been recognised in the Nelson Bay Local Fauna, but was not known at the time of Flannery and Hann's (1984) description.

The identification of the posterior incisor as I² rather than I³ is based on the following observations. In all grazer and intermediate grazer-browser macropodines, I³ is relatively elongate anteroposteriorly and divided into two lobes by a labial groove, which is positioned approximately

centrally or towards the posterior (Ride 1957). In contrast, I² is narrower and not divided into two lobes, with the short groove occurring very close to or on the posterior margin of the tooth. Flannery and Hann (1984) described NMV P173591 as an I³ based on its superficial similarity to I³ of *Onychogalea unguifera*. But even in the latter species, where the posterior incisors are very reduced and narrow, I³ still possesses a labial groove, which is positioned approximately centrally. The unworn *B. nelsonensis* incisors described above are more consistent in morphology with that of I².

Examination of the much larger sample of *B. nelsonensis* material from Nelson Bay has shown there is little morphological variation within the species, and all other specimens are consistent with the holotype and referred specimens.

Unfortunately none of the upper incisors have been found in association, either with each other or with other *B. nelsonensis* material. Due to the lack of more complete maxillae or premaxillae material, details of the palate and the shape of the incisor arcade are still unable to be described.



Figure 2. *Baringa nelsonensis*. NMV P201156 right adult dentary, lateral view. Scale bar = 10 mm.

CURRAMULKA LOCAL FAUNA 'BARINGA'
SPECIES

Two species from the early Pliocene Curramulka Local Fauna, Yorke Peninsula, South Australia were tentatively allied with *Baringa* by Pledge (1992).

The first species, cf. *Baringa* sp., is about 30% smaller than *B. nelsonensis* from Nelson Bay. It was referred to *Baringa* on the basis of similarities in the dentary shape, depth of the buccinator groove and morphology of P_3 (Pledge 1992). Our re-examination of these specimens can confirm the possession of only the first of the features used by Flannery and Hann (1984) to diagnose *Baringa* (i.e. a well-developed crest on the dentary just ventral to the ventral rim of the masseteric foramen). In cf. *Baringa* sp. the anterior cingula on the lower molars are much shorter and broader than those of *B. nelsonensis*, and the I_1 is relatively narrower dorso-ventrally, and possesses a more horizontally-inclined wear facet.

Compared to *B. nelsonensis*, which possesses only two intermediate cuspules, the P_3 of cf. *Baringa* sp. differs in possessing three intermediate cuspules with more defined associated ridgelets. The lower deciduous premolar, dP_2 , also differs in lacking the small anterior and posterolingual cuspules present in the dP_2 of *B. nelsonensis* described in this paper. An unusual feature of this Curramulka species is the presence of a small shelf-like posterior cingulum or bulge on at least the M_3 and M_4 of some of the specimens (e.g. SAM P31337, SAM P29863). Pledge (1992) noted that the dentary was even in depth below the teeth in cf. *Baringa* sp., a feature he used to ally it to *B. nelsonensis*. However, the dentary of *B. nelsonensis* is deeper below M_1 than M_4 (Flannery and Hann 1984). The P^3 of cf. *Baringa* sp. also possesses a lingual cingulum which is better developed, although only very slightly, than that seen in *B. nelsonensis*.

Cf. *Baringa* sp. appears instead to be closer to *Thylogale*, which is phenetically similar to *Baringa* (Flannery and Hann 1984), particularly in the morphology of the premolars and lower molars, but is smaller. In particular, the Curramulka Local Fauna specimens are most similar to extant *T. stigmatica* in the relative length of the premolars to the molar row, and to the extinct *T. ignis* from the Early Pliocene Hamilton Local Fauna (Flannery et al. 1992) in the form of the premolars (i.e. presence of three intermediate cuspules on the main blade, a small cingulum around the base of the teeth, a low posterolingual cusp and the lack of a distinct lingual cingulum on P^3). The similarity of the specimens to *Thylogale* was noted by Pledge (1992), however he considered them closer to *Baringa* based on features

of the dentary. We believe these features differ significantly from those of *B. nelsonensis* and suggest the specimens of cf. *Baringa* sp. be referred to cf. *Thylogale* sp. pending a more thorough review of the Curramulka Local Fauna macropodids.

The second species described by Pledge (1992), cf. *Baringa nelsonensis*, is similar in size to the Nelson Bay specimens. However, as in cf. *Baringa* sp., it resembles *Baringa* only in the possession of a well-developed crest on the rim of the masseteric foramen. Cf. *B. nelsonensis* also differs from the type series of *B. nelsonensis* in having: a dentary that is even in depth below the teeth; the ascending ramus inclined slightly less vertically; a smaller I_1 that is shallower dorsoventrally, and has a more horizontal wear facet; shorter and broader anterior cingula on the lower molars; a longer dP_2 that lacks the small anterior cuspule; a larger P_3 that is more rectangular in shape; a dP^2 with a very well-developed lingual cingulum forming a shallow basin, and a well-defined intermediate cuspule and posterior fossette; a P^3 with a better-developed lingual cingulum, a deeper groove separating the posterolingual cusp from the posterior cusp, a well-developed posterior fossette, and the three intermediate cuspules on the main blade sub-equal to, rather than lower than, the anterior and posterior cusps. In some respects the P^3 is similar to that of *Petrogale* spp. and the dP^2 is similar to that of *Wallabia bicolor*. Cf. *B. nelsonensis* may represent an as yet unknown genus or species, but it is unlikely, for those reasons listed above, to be referable to a species of *Baringa*.

DISCUSSION

Flannery and Hann (1984) suggested that the lower incisors of *Baringa nelsonensis* might have been used to scrape off bark or lichens, or to sever hard plant stems. The enlarged crest on the rim of the masseteric foramen, and excavated jugal also noted by Flannery and Hann (1984), indicate the presence of an enlarged masseter muscle. This suggests that *B. nelsonensis* possessed an increased ability to move the dentaries anteriorly when compared to other macropodines (Sanson 1980; Flannery and Hann 1984). Although the upper incisors have not been found in life position, their relative sizes and other general browsing features of the dentition suggest the I^1 probably extended below the occlusal line of I^{2-3} (Sanson 1989). The anterior movement of the dentaries would bring the lower incisors into occlusion with the large, robust I^1 s, giving a possible mechanism for the production of the vertical wear facet observed on the lower incisors.

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Observations on the stage of eruption and wear of molars associated with lower incisors supports Flannery and Hann's (1984) hypothesis that the majority of incisor wear occurs after the eruption of P_3 , although some wear is seen to occur while dP_2 is still part of the functional dentition (Herrmann 2000), indicating that the specialised feeding style described above is initiated early in the animal's life.

Strong morphological similarities are observed between the I^1 s of *B. nelsonensis* and *Protemnodon*, as well as in the wear patterns observed on the lower incisors. The vertical wear pattern, one of the diagnostic characters of *Baringa*, has also been seen in some species of *Protemnodon* (Flannery and Hann 1984), and in the recently described *Silvaroo bila* (Dawson 2004). No I^1 s are known for *Silvaroo*, however it is likely that they would also be relatively robust and enlarged relative to the cheek teeth, and that the feeding habits of *Silvaroo* may have been similar to that of *Baringa*.

The most complete *B. nelsonensis* dentary from Nelson Bay, NMV P201156 (Fig 2), was found with I_1 attached in an apparent life position. This specimen therefore appears to have a relatively elongate diastema (94% the length of the cheek tooth row in *B. nelsonensis* compared to 75% in *Thylogale billardierii*), a feature usually associated with grazers (Ride 1959; Dawson and Flannery 1985). *Baringa nelsonensis* otherwise possesses dental features more indicative of browsing macropodids, i.e. narrow anterior cingula and weak midlinks on molars, moderately low-crowned molars, relatively large premolars, no evidence of molar progression, and only a very slightly curved lower tooth row, resulting in the eventual occlusion of both the anterior and posterior cheek teeth at the same time (Sanson 1980, 1982, 1989). However, the lack of a lingual valley on the P^3 , and transverse striations on the molars indicating lateral movement of the lower jaw during mastication suggest that abrasive vegetation may also have been a part of its diet (Sanson 1980), possibly on a seasonal basis.

If, as argued here, the Curramulka Local Fauna specimens are not referable to *Baringa*, the extension of the range of *Baringa* to the Early Pliocene by some workers (e.g. Tedford 1994) is no longer supported, returning its only named occurrence to the early Pleistocene. Interestingly, an un-named macropod from the Plio-Pleistocene Nullarbor Caves possesses upper incisors that bear a strong resemblance to those of *Baringa* (J. Long pers. comm.). This material is very well preserved and includes complete skulls and associated postcranial material. If this material is referable to *Baringa* or a new closely-related

genus, it will add considerably to our knowledge of this extremely unusual macropod and its unique adaptations.

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Specimens of *Baringa nelsonensis* from Nelson Bay examined and discussed in the text

NMV P173648 right I¹; NMV P200659, partial right I¹; NMV P200685, partial left I¹; NMV P216022, left and right I¹; NMV P 216023, tip of right I¹; NMV P216024, left I¹; NMV P216026, right I¹; NMV P216027, left and right I¹; NMV P216028, right I¹; NMV P216032, left and right I¹; NMV P216035, worn left I¹; NMV P216036, right I¹; NMV P216145a, right I¹; NMV P216221; partial left I¹; NMV P173591, right I²; NMV P200702, left I²; NMV P215806, left I²; NMV P215810, left I²; NMV P215811, right I²; NMV P215992b left I²; NMV P216202, left I²; NMV P216224, left I²; NMV P200444, left dP² (associated with left dP³, M¹⁻²); NMV P200482, left dP²; NMV P200490, anterior cusp of left dP²; NMV P215774, left dP² (in maxilla fragment also containing left dP³); NMV P215794, right dP²; NMV P215966, right dP²; NMV P216888, right dP²; NMV P201155, isolated left dP² and right dP₂ (associated with isolated left and right dP³, M¹⁻², left and right I₁, dP₃, M₁₋₂, unerupted left and right M₃, right P₃); NMV P215777, isolated right and left dP², and left dP₂ (associated with isolated left and right I₁, isolated right P₃, left dP₃, M₁₋₂ and unerupted P₃ and M₃ in partial dentary, right M₁₋₂ and unerupted M₃ in partial dentary, isolated left P³ and left dP³, left M¹⁻² in maxilla fragment, right dP³-M¹ in maxilla fragment); NMV P200410, left dP₂ (in dentary fragment with dP₃, M₁₋₂, associated with I₁); NMV P200449, right dP₂; NMV P200450, partial left dP₂; NMV P200690, partial left dP₂; NMV P215789, right dP₂; NMV P215790, right dP₂; NMV P201156, partial dentary containing I₁, P₃, M₁₋₄.